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Introduction

There was nothing where now are earth, sun, moon, stars and all that we see. Ages long the darkness was gathering until it formed a great mass in which developed the spirit of Earth Doctor, who, like the fluffy wisp of cotton that floats upon the wind, drifted to and fro without support or place to fix himself. Conscious of his power he determined to try to build an abiding place, so he took from his breast a little dust and flattened it into a cake. Then he thought within himself, "come forth, some kind of plant," and there appeared the creosote bush.

From the Pima Creation Myth

To the Pima Indians of the Sonoran Desert it was revered as the first plant on earth. The Spanish called it *gobernadora,* "the governess." These perceptions of the creosote bush embody two essential truths about this remarkable plant. As Gwen Waring describes in this special issue of *Agave,* individual creosotes rank among the oldest plants of the North American desert. The creosote is also the dominant one — thriving as does no other plant in the Chihuahuan, Sonoran and Mojave deserts.

People of our world today rarely have neutral feelings about the creosote bush. Many regard it as common, ugly and worthless. To others, it personifies the desert itself, delicate and graceful in form yet tough and persistent — the ultimate desert survivor.

This issue came about as a result of a gift from Samuel Sutton, who seeks to promote greater understanding of "my favorite plant, the creosote bush." It is our hope that this article will stimulate your thinking about this plant.

Read this issue, then take another look at the creosote bush. If you still find it unimpressive, try something else — after the next summer thunderstorm, close your eyes ... breathe deeply ... and smell the creosote-covered desert. Then you may reconsider and come to know "the governess."

Robert G. Breunig, Ph.D.
Executive Director

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Creosote Bush: The Ultimate Desert Survivor

by Gwen Waring

GETTING TO NORTH AMERICA

The Evolutionary History of Creosote Bush in North America

Creosote bush is the persistent shrub that seems to go on forever across the bajadas and valley floors of the southwestern deserts. The intent of this article is to reconstruct the ancient history of this fascinating plant — where it came from and how it has migrated and adapted to the habitats it has come to occupy, namely a large part of the North American Southwest. Creosote bush is known as *Larrea tridentata* in the family Zygophyllaceae. The family is a small one with world wide distribution and is comprised mainly of species which are well-adapted to life in the desert. One species, *Augea capensis,* a succulent, is one of the few plant species encounted in the deserts of South Africa where there may be no rain for years on end (Hutchinson 1967).

Creosote bush (*Larrea* spp.) itself occurs only in the New World, where there are five species. One of these alone, *L. tridentata,* has come to live in North America, in three of the four western deserts (Chihuahuan, Sonoran, Mojave) and the northern half of Mexico, representing a very large range of hundreds of thousands of square miles. The other four species of creosote bush occur only in South America, in Argentina, Chile and Peru, with several species extending as far north as Bolivia. All five species look alike superficially, indicating that they are closely related. But through the process of evolution they have diverged considerably genetically in leaf, flower and fruit morphology and in the chemicals they produce, including proteins and phenolic leaf resins, giving rise to a group of very different species. Several species are adapted to wetter and milder or more mesic environmental conditions, while the other two have adapted to live in deserts, as has *Larrea tridentata* (Mabry et al. 1977). Knowledge of these traits has provided us with information about the evolutionary history of our northern creosote bush.

Some clones of the creosote bush in the Mojave Desert may be up to 11,700 years old. This aerial photo shows the large rings called "fairy rings."
Photo by Dr. Frank Vasek

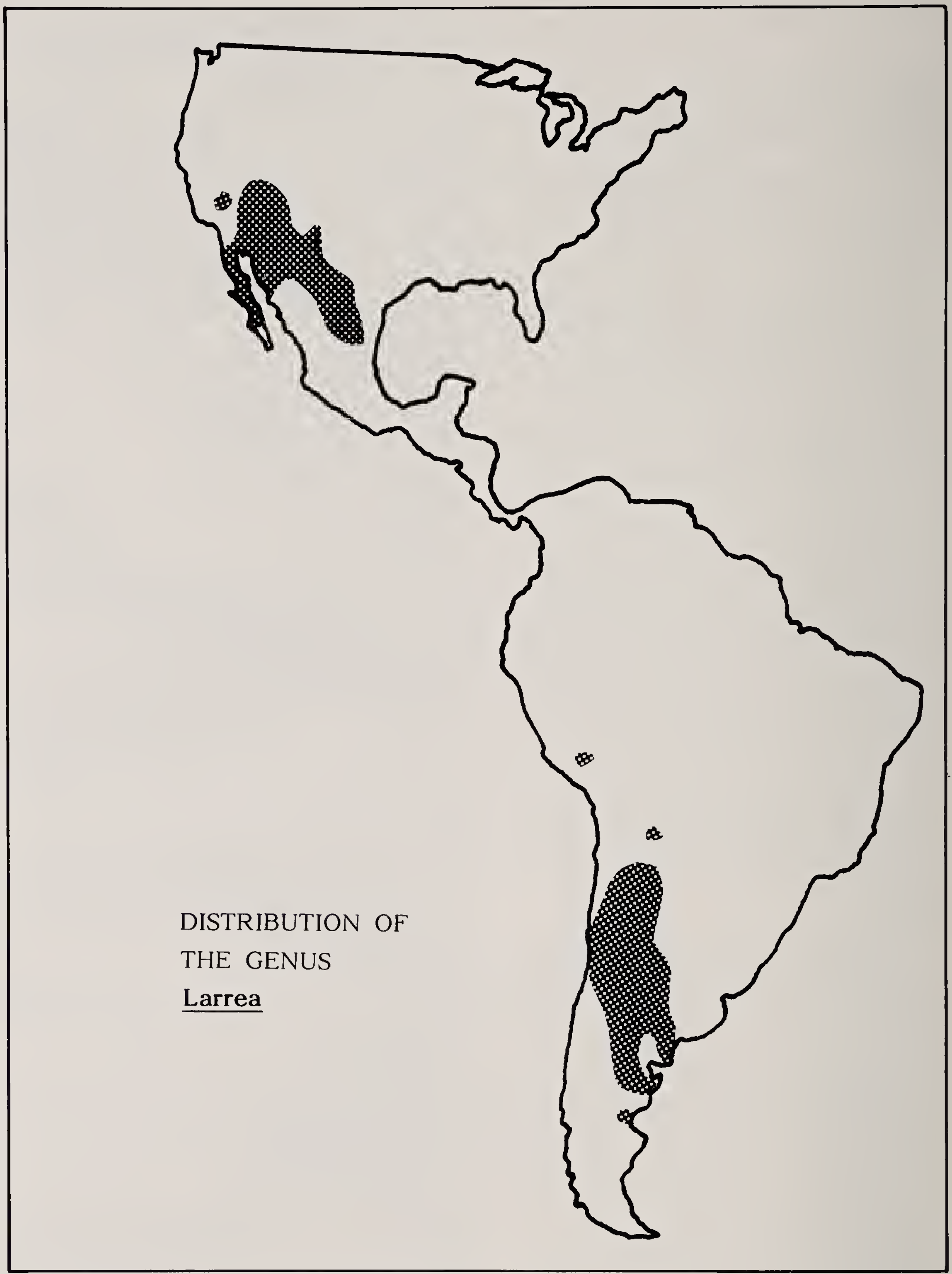
The closest relative to and probable ancestor of *Larrea tridentata* is *L. divaricata,* one of the South American species whose current range extends up to southern Bolivia. Because these two species are compatible sexually and the most similar morphologically and in their biochemistry of all the *Larrea* species, most scientists regard them to be either the same species or very closely related subspecies, which are in the process of diverging. *L. tridentata* and *L. divaricata* are more closely related to and more compatible with one another than *L. divaricata* is to other creosote species which co-occur with it in South America. Yang et al.

(1976) determined through hybridization studies that these two species are starting to diverge, although they are very closely related. Although they have homologous or compatible chromosomes, many of their hybrid offspring do not produce viable pollen or seeds.

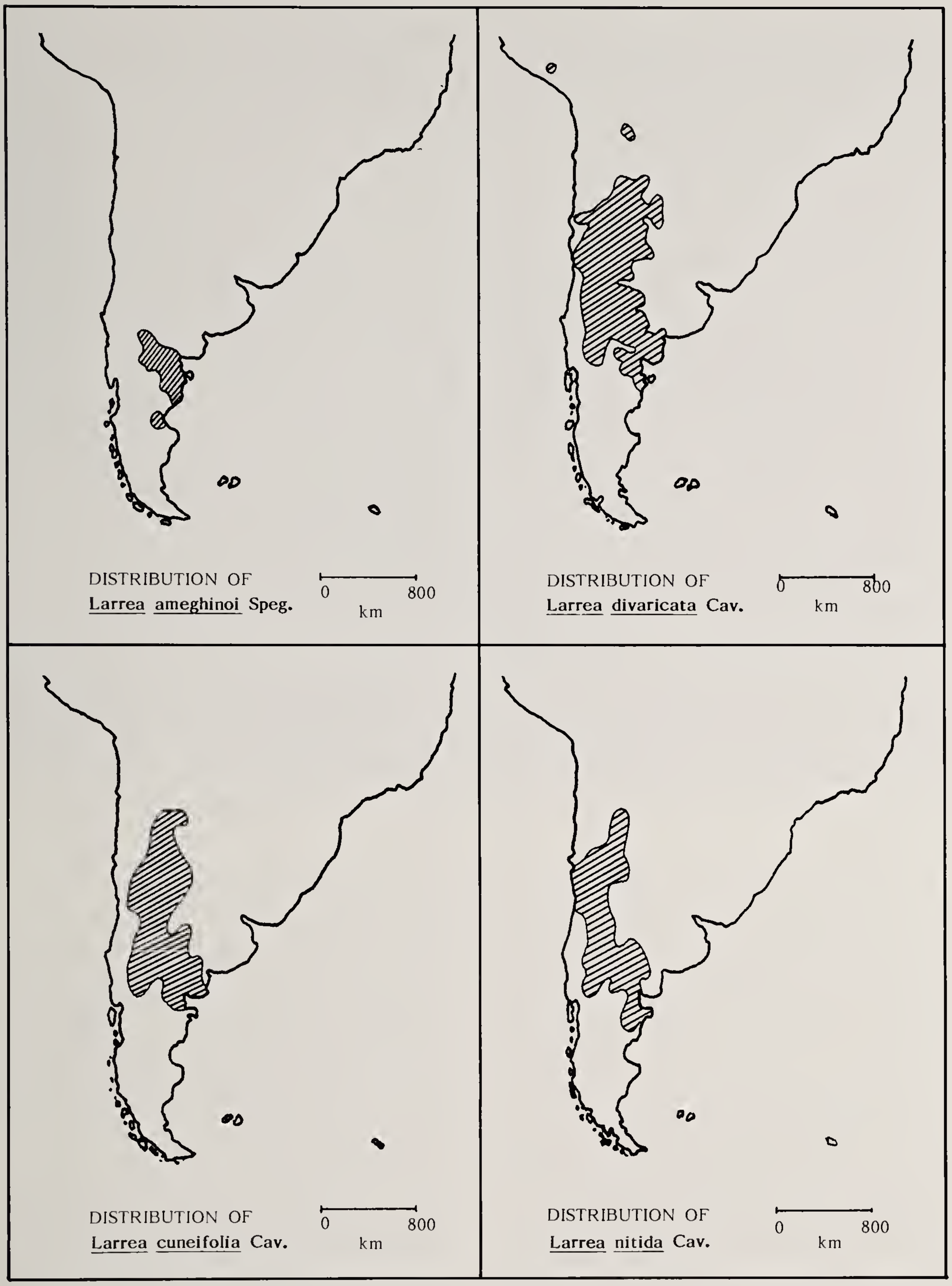
Because there are more species of *Larrea* in South America than in North America and *L. tridentata* is more similar to one of them than they are to one another, it has been proposed that creosote bush originated in South America and subsequently migrated north to North America (Mabry et al. 1977). This is suggested because the presence of more species of *Larrea* in South America implies that they have occurred there longer and have had more time to evolve the differences which they exhibit. And the lack of major differences between *L. divaricata* and *L. tridentata* suggests that the latter has diverged more recently from the group than others.

Some scientists believe that creosote bush may have actually originated in North America and subsequently migrated south (Porter 1974, Turner 1973). This perspective is based partly on the fact that a genus (*Sericodes* sp.) which is very similar morphologically to *Larrea* occurs only in North America (Porter 1974). However, recent genetic studies of *Sericodes, Larrea* and other genera in the family Zygophyllaceae indicate that *Larrea* is more closely related to South American species in the family (Mabry et al. 1977, Yang et al. 1976), which renders this view no longer tenable.

The migration of creosote bush from South to North America probably occurred within the last 3 million years, during the late Pliocene. We know that it probably did not arrive here sooner because it was only then that the two continents became joined, due to island building and then the formation of a land bridge, which are now represented by Central America. When these two continents united there was a major interchange of plants and animals (Stehli and Webb 1985) and with this, creosote bush was destined to become an important component of the flora in the southwestern deserts of North America.



An interesting puzzle in this story lies in the fact that we do not know precisely how creosote migrated to North America because populations of *L. tridentata* and its ancestor, *L. divaricata,* are separated by more than 3,000 miles. Creosote bush does not occur between central Mexico and northern Bolivia, an area which is comprised largely of tropical habitat much too wet to be colonized by this desert dwelling species. While we do not know for certain how creosote bush was able to cross this very long distance of thousands of miles, several interesting explanations or hypotheses have been offered, based on available information. The plant's seeds have very hairy coats and they can catch in animal hair or feathers. Because of this, seeds of the plant may have been transported on the feathers (or in the digestive tracts) of birds which migrate between South and North America. While this seems, intuitively, very implausible, birds have in fact been implicated in dispersing seeds of some plants to places as remote as the Hawaiian Islands (Carlquist 1967). The dispersal of plants throughout the history of life has probably involved countless such "implausible" events.



Another possibility is that there was once a continuous expanse of creosote bush between North and South America and subsequent climatic or geological events drove the intermediate populations to extinction. This hypothesis has support in the fact that over 150 populations of other plant species, many of which are desert dwellers, also have disjunct or discontinuous distributions between North and South American deserts, particularly the Monte region of Argentina and the Sonoran Desert (Raven 1972). Many of these species are the most important in terms of abundance in both desert regions and both deserts are remarkably alike climatically (Solbrig 1972). Among these species are gray thorn (*Condalia* spp.), paloverde (*Cercidium* spp.), large cacti (*Cereus* spp.), hackberry (*Celtis* spp.) and mesquite (*Prosopis* spp.). All of these species may once have had continuous populations at least along an arid corridor in this land bridge between the two continents, only to be divided later by some major event which produced the wet tropical region which now divides them. It is noteworthy that there are some arid-adapted animal species, including rattlesnakes, whose populations are also separated by the Central American tropics (Webb 1978), making it unlikely that long distance dispersal by birds could account for all the existing disjunctions. We may never know what happened for certain, but creosote bush's distribution clearly shows us something of the dynamic nature of this plant's evolutionary past.

Upon Arriving in North America

By arriving in North America within the last 3 million years, creosote would experience some extreme weather conditions. An epoch called the Pleistocene would begin soon (about 2.2 million years ago) and with it came at least four major ice ages, which retreated for the last time only about 10,000 to 11,000 years ago. During this time the world's climates cooled, and in North America glaciers extended down into what is now the northern United States. In Arizona a mountain glacier formed on the San Francisco Peaks to the north and the southern deserts cooled. When this happened, many plants which now occur in the Sonoran Desert migrated or retreated into Mexico to lower, warmer elevations and were replaced by more cold-tolerant species such as pinyon, junipers and oaks. Thus, the complexion of the Sonoran Desert as we know it changed radically during the Pleistocene.

There were also interglacial or warmer periods during the Pleistocene, and in the southwestern deserts such as the Sonoran Desert the glacial and interglacial periods resulted in plants and animals migrating up and down latitudinally and elevationally at least several times in response to the alternating cold and warm conditions. So while many species have been in the Sonoran Desert for a long time, their stay has been a very dynamic one. This was also true for creosote bush.

Paleontologists and geologists have learned of these events by use of a process called radiocarbon or carbon 14 dating, which they have used to age organic material such as preserved dung and packrat (*Neotoma* spp.) middens or nests which are suspected to be ancient. All organic material contains radioactive carbon atoms

(14C) and carbon atoms, like other isotopes, decay or lose electrons as they age. With complicated equipment and a knowledge of the rate at which 14C decays, scientists can date such material with considerable accuracy. These techniques have been particularly useful in the southwest where the aridity preserves organic material for tens of thousands of years. Dung samples are commonly found in caves that once sheltered large mammals. Packrats, like some people, accumulate a large array of litter and their middens provide good records of what plant species were present at a given time. With this information, paleontologists have been able to describe climatic conditions of much earlier times in the earth's history.

The oldest date for creosote bush in the Southwest is about 40,000 years before present (b.p.). Pieces of cuticles from creosote leaves were collected from Shasta ground sloth (*Nothrotheroips shastensis*) dung found in Rampart Cave in the lower, western end of the Grand Canyon and the dung was then radiocarbon dated to give this date (Hansen 1978). So 40,000 years ago creosote bush migrated that far north, probably along the Colorado River. The period from about 50,000 to 25,000 years ago was a relatively warm Pleistocene interglacial stretch of time during which creosote bush and other desert plants expanded their ranges north while mesic plants receded even farther north to higher elevations and cooler climates. Following this, another glacial advance set in and the deserts again cooled. With this cooling event, no evidence of creosote bush in the southwestern deserts was found until about 18,000 years b.p. This date came from a packrat midden east of Yuma, Arizona, which was collected and radiometrically dated by Dr. Tom Van Devender, a paleontologist at the Arizona-Sonora Desert Museum. Van Devender extracted fragments of creosote plants in samples from this midden and then dated the woody portions of the midden. Following this, creosote bush is commonly found in middens in the southern parts of southwestern deserts dating from 10,000 to 11,000 years to the present,

In this Vasek photo the arrow indicates the ring he called "King Clone" which is 27 ft. in diameter.

while in the northern parts of the Mojave and Chihuahuan Deserts, which occur at higher elevations, it is not represented in middens prior to 4,000 to 5,000 years ago. This suggests that the cooling effects of the Pleistocene lingered into the Holocene and the desert was slowly expanding to its modern range.

During the warmer interglacial periods, creosote bush migrated across the North American deserts from the Chihuahuan Desert through the Sonoran Desert to the Mojave Desert. In the process, its genetic makeup changed dramatically and remains so today (Yang 1970). The number of chromosomes in creosote bushes increases across the deserts from east to west. That is, the DNA strands which contain these plants' genetic information and heritage are totally duplicated so that while plants in the Chihuahuan Desert have the original number of chromosomes, those in the Sonoran Desert have doubled to yield 26 chromosomes, and tripled in the Mojave Desert where creosote bushes have 39 chromosomes (Yang 1970). This phenomenon of chromosome doubling, tripling, etc., is called polyploidy. It is thought that most flowering plants arose through this process, so polyploidy is a very important source of variation in plants. A change in the number of a plant's chromosomes changes the way a plant is in a variety of ways, and very commonly polyploidy is associated with a plant's move into harsher environments, whether they be hotter, drier or colder (Grant 1981). According to Clark Schaack (personal communication) a biologist at Northern Arizona University, an octaploid individual (52 chromosomes) has been located in northern Arizona, at a higher elevation, where cold temperatures may be stressful.

These three plant groups in the three southwestern deserts have diverged in some morphological and physiological characteristics, probably due to the change in ploidy level. As creosote plants increase in ploidy levels from east to west, they tend to: produce fewer stomates or pores in their leaves (which reduces water loss from the leaves); the leaves change in shape, increase in thickness and become more pubescent or hairier; fruits

Each clone is an individual plant. They grow out from the center to form the large rings. Vasek photo.

become smaller; stems branch less; and plants are generally shorter (Mabry et al. 1977). Some of these traits are genetically controlled and may be adaptations derived from the polyploid state which have enabled this species to invade progressively harsher environments where temperatures soar and water is scarce.

As creosote bushes re-invaded the southwestern deserts with the close of the Pleistocene, it appears that many individuals stayed put and persisted for periods of time previously not thought possible for plants. According to Dr. Frank Vasek, a botanist at the University of California, Riverside, some clones of creosote bush in the Mojave Desert may be up to 11,700 years old (Vasek 1980). If so, these may be the oldest living organisms on earth. To ascertain this, Vasek found some very large creosote bush clones (each clone is an individual plant) in the Mojave which had grown out from the center to form large rings referred to as "fairy rings." He collected dead stems from the interiors of the rings and radiocarbon dated them. With this information and a knowledge of growth rates of the plant, he estimated that one fairy ring, which is 27 feet in diameter, was nearly 11,700 years old. He named this clone "King Clone." This persistence indicates how well adapted this plant is in its tolerance of highly variable environments.

During the Pleistocene, a variety of very large grazing and browsing mammals, including mammoths, mastodons, camels, horses and giant ground sloths, roamed North America. They fed on plants from Arizona to Alaska throughout the Pleistocene up until about 10-11,000 years ago when they disappeared from North America. There is some evidence, direct and indirect, that creosote bush was a food source for some of these large ancient creatures. As already mentioned, the remains of creosote leaves were extracted from Shasta ground sloth dung from the Grand Canyon and dated at about 40,000 years, indicating that this creature browsed the plant at least occasionally. It is generally accepted, however, that the Shasta ground sloth relied more heavily on other plant species such as globe mallow (*Sphaeralcea* sp.) and Mormon tea (*Ephedra* sp.) for food (Thompson et al. 1980).

While the fossil record is limited for information on the use of creosote bush as a food resource by the Pleistocene megafauna, several more contemporary associations may shed some light on the subject. In the 1850's a U.S. Army expedition led by Edward Beale came west through Arizona, charged with exploring new routes to California. The expedition relied on camels (*Camelus* sp.) imported from the Middle East to transport their supplies. The camels ate creosote bush, along with everything else, with voracious appetites, and actually thrived on them, much to the amazement of the explorers (Faulk 1976). Because the American camel (*Camelops* spp.) was native to the Southwest in the Pleistocene, it, too, may have fed on creosote then. Along the same lines, feral burros (*Equus asinus*) in the Southwest (introduced into the United States by the Spanish) are known to browse to some extent on creosote bush (Woodward and Ohmart 1976), although other food plants are preferred. The earlier, native species of horses (*Equus* sp.) may also have browsed creosote bush. All in all, creosote bush seems to have marched through geologic time in North America with little to no threat of being overgrazed, and some of the reasons for this will be addressed later. This lack of major herbivore pressure on this plant has probably contributed significantly to its successful establishment in the Southwest.

Pondering the evolutionary history of the creosote bush suggests an enticing story. It reveals not only how complex the life history of a species can be, but also sheds some light on the process of scientific exploration. This newcomer desert species made a large jump to North America by means which we may never know. It survived the stressful weather extremes of the Pleistocene and stayed on to successfully colonize and help define the North American deserts, due in part to evolutionary adaptations to new environments and a life history which enables individuals to persist for thousands of years.

Creosote bush has been called the most drought-tolerant plant species of the desert and the most widely distributed perennial plant ir

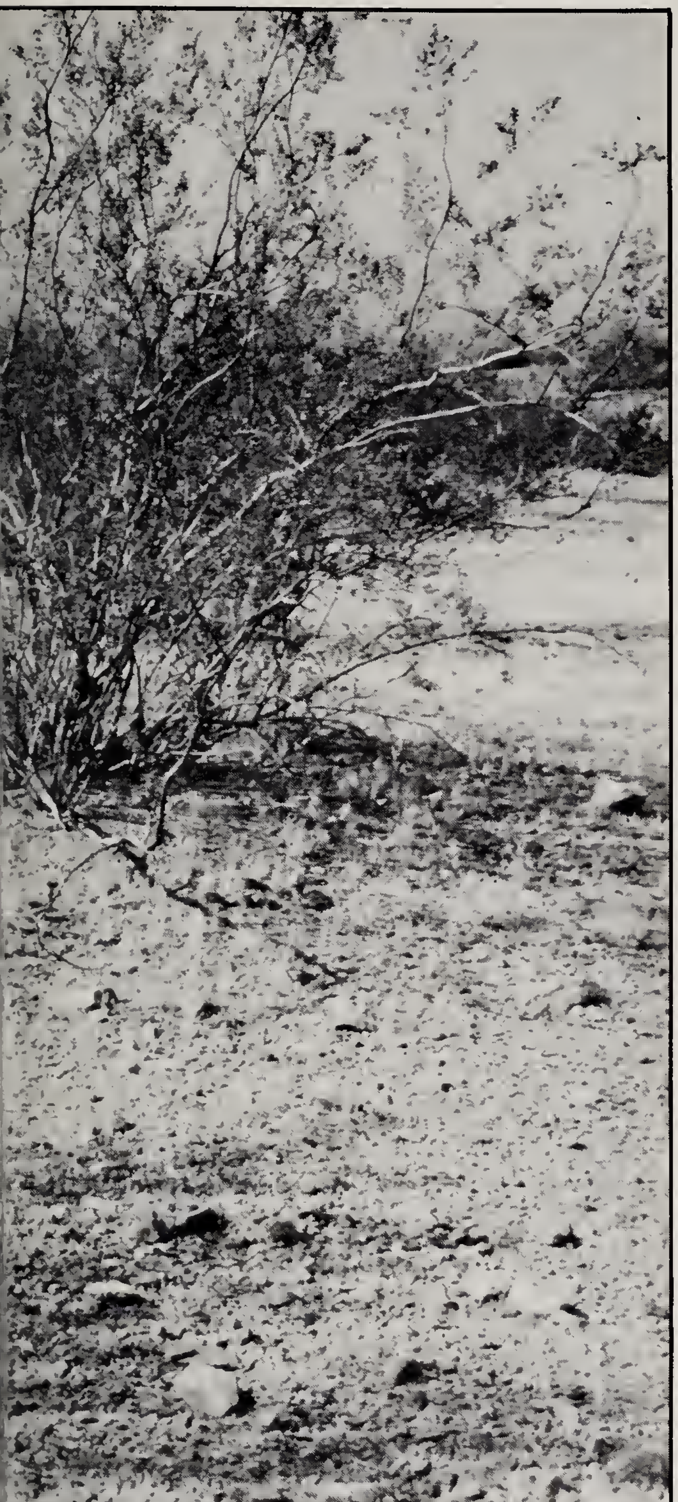
A REMARKABLE TOLERANCE OF THE DESERT

The Ecological History of Creosote Bush in North America

As the Pleistocene ice and cold receded to the north, creosote bush expanded its range into a desert that would become hotter, drier and more extensive than it had ever been before (Axelrod 1979). One can almost imagine this plant on the move ... a carpet of seedlings growing and thriving in a blistering landscape abandoned by pines, junipers and oaks. The Sonoran Desert was recolonized by many desert species after the Pleistocene, but by none more successfully than creosote bush. This is evident now, for it is creosote's yellow flowers and fragrant scent which predominate each spring when the desert comes alive, and its green branches that wave in the wind when summer comes along and little else offers up the color green.

This plant is rightfully lauded for its ability to live and, indeed, thrive, in the desert. This aspect of creosote's natural history fascinates scientists and consequently it is well-studied. Creosote bush has been called the most drought-tolerant plant species of the desert (Barbour 1968) and the most widely distributed perennial plant in the southwestern deserts (Runyon 1934). Its distribution has been used to define the boundaries of our southern deserts. Shreve (1940) maintained that no part of North America was too hot or too dry for creosote bush. According to Shreve and Wiggins (1964) *Larrea* has successfully colonized areas which may not receive rain for up to a year at a time. Summer temperatures in the North American deserts commonly exceed 100° F every day. Together with a lack of rain, this precludes all but the hardiest species, yet creosote bush thrives here.

Desert plants such as the cacti have impressive adaptations for rapidly collecting and storing large amounts of water to sustain them through seasonal dry spells. Succulents, such as agaves



he southwestern deserts.

and yuccas, as well as the cacti, avoid opening their stomates (the pores in their leaves) to take in CO_2 needed for photosynthesis of carbohydrates until nightfall, thereby avoiding evapotranspirational loss of water. Acacia and mesquite trees have tap roots deep enough to reach ground water. Desert annuals germinate, develop and reproduce during the cooler, wetter spring months and are back as dormant, impermeable seeds in the soil before summer conditions bake the deserts dry. Creosote bush has evolved few of these water conservation or storage strategies: instead, it simply gets by with less water.

To survive in the desert, plants must be able to continue photosynthesis under drought conditions. By doing this a plant produces the energy it needs to live, for in photosynthesis, carbohydrates, which are an excellent source of energy, are produced. As plants become water stressed, they cannot open their stomates to take in CO_2 because, if they do, they lose leaf water to the atmosphere. Under these conditions many desert-adapted plants, such as the ocotillo, simply drop their leaves and become dormant until water becomes available. More delicate plants, which are not desert adapted, simply wilt and die, much as a house plant which is underwatered, because this extreme dessication can cause permanent damage to plant cells. Creosote, however, does not drop all its leaves and is able to tolerate severe levels of water loss for several reasons.

Even during hot, dry periods, creosote bush can photosynthesize actively. In several tests it was able to continue photosynthesis at greater levels of water stress than other desert species such as brittle bush (*Encelia farinosa*) or desert willow (*Chilopsis linearis*) (Mabry et al. 1977). Creosote bush has several morphological features which contribute to this tolerance: its small leaves reduce surface area and potential heat load; water stressed plants produce more leaf resins, which may reduce water loss; this species is very efficient at reducing transpirational water loss through its leaves; and, perhaps most intriguingly, creosote bush can tolerate very low levels of water in stems and roots. The significance of this is worthy of elaboration.

For a plant, the process of drawing water from the soil depends on an osmotic imbalance in water levels between the soil and the roots of the plants. If plants are water stressed, there is really less water in the soil than in the tissues of the plant's roots, so if anything, the plant will have to protect against water moving out of the plant and into the soil. If soil water is not available, the cells and then the entire plant may simply wilt and die if the plant is not adapted to tolerate dessication. Desert perennials can tolerate water stress better than, for example, water cress or most garden plants. Desert plants have evolved adaptations which enable them to function and maintain their structure when less water is available. The real value of this comes in the fact that with less water in their root tissues, the better they get at drawing water from progressively drier and drier soils. All plants have their limits, however. As summer heat and drought increase in the southwestern deserts, even hardy desert species such as wolfberry (*Lycium* spp.), paloverde (*Cercidium* spp.), ocotillo (*Fouquieria splendens*) and brittle bush (*Encelia farinosa*) begin to drop their leaves and go into a state of dormancy. Creosote bush, however, continues to photosynthesize, in part because of its amazing ability to draw water from seemingly dry soil. Perhaps its most important adaptation is that its protoplasm, or cell material, can recover from this dessication without permanent damage (Ashby 1932). We don't as yet fully understand the nature of this process.

Larrea successfully colonizes harsher habitats because it also exhibits considerable plasticity in its growth form. When found growing on carbonate deposition layers (caliche) it rarely exceeds three feet in height, because the soil layers on these caliche beds are so shallow that they hold little water. However, when creosote grows in deeper soils, its height commonly exceeds five or six feet because these soils hold more water (Cunningham and Burk 1973, Waring, unpublished data). Shreve and Mallery (1933) proposed that precipitation and caliche together regulate local densities and height of creosote bushes. "Areas of *Larrea* in Cochise Co., Arizona, at an elevation of 4,000 ft. (1220 m), with an approximate rainfall of 14 inches (355 mm), but with soil heavily impregnated with caliche 15-25 cm from the surface, have been compared with areas in the District of Altar in Sonora, Mexico, at an elevation of 1,600 ft. (488 m), with an annual rainfall of 9 inches (288 mm), but on soil free of caliche. In spite of the higher rainfall in Arizona, the stand of *Larrea* is much heavier and the plants much taller in Sonora." (Shreve and Mallery 1933.)

CREOSOTE BUSH AND OTHER DESERT PLANT SPECIES

Because of its ability to tolerate dessication, creosote bush often occurs in monospecific stands in the drier parts of the Southwest. While some people think that creosote bush occurs this way because it is excluding other plant species, either by direct root competition for water or the production of toxins which make the soil around the plant uninhabitable, there is little direct evidence that this is the case. Rather, it is because creosote bush can tolerate conditions that most other desert plants cannot that it often occurs alone. Many of these areas, such as the caliche deposits of the Verde Valley or the endless sandy flats of the Mojave Desert, are extremely water limited and might otherwise go uncolonized. From Texas to California, creosote bush co-occurs with fewer and fewer other plant species because there is less rainfall in the western deserts (Mabry et al. 1977). One can easily imagine a long, hot sweaty drive through endless miles of creosote flats. It is somehow reassuring to know that at least one species can overcome such harsh environments.

In the Mojave Desert, creosote bush and another extremely drought-tolerant species, bursage, *Ambrosia dumosa,* co-occur. Together these two species dominate most of this hottest and driest of North American deserts. Through removal experiments, Fonteyn and Mahall (1981) determined that these two species do compete with one another for water. By removing one species or the other from plots, they found that the remaining species became less water stressed, while if plants of the same species were removed, there was less change in water stress, suggesting that more water had become available for roots due to the removal of the other species. Even though these hardiest of species appear to compete for water, they do still co-occur.

Other plant species are often found growing adjacent to creosote bush in wetter areas. This creosote and juniper relationship is an example.

Other desert species are often found growing adjacent to creosote bush in wetter areas. A preliminary survey revealed that over 15 species of native plants have been found growing next to creosote bushes or under their canopies, indicating that creosote does not exclude other species. Among these are paloverde, mesquite, acacia, false paloverde, various cacti (including the saguaro, barrel cacti, chollas, prickly pear, christmas cacti), rabbit brush, brittle bush, heron's bill, many grasses, ocotillo, etc., (Waring, personal observation).

Creosote bushes often act as "nurse plants" for many native plant species. Cactus seeds rarely germinate in sunny open patches, but rather in the shade of plant canopies where there may be more water and nutrients available and less exposure to radiation or herbivores. In drier years, most annual plants are found only under the shade of plants such as creosote bushes. These relationships can be negative ones for creosote bushes (Yeaton 1978), because other plants are moving in to use its water and sunlight. Nurse plant associations are frequently observed throughout the Sonoran Desert, especially in Organ Pipe National Park and Saguaro National Monument East in Arizona. This suggests that creosote bush is not an aggressive competitor, but rather an opportunist of sorts, which can colonize habitats too harsh for many species and which co-occurs with them in more temperate regions. An exception to this may be the colonization of cattle rangelands in New Mexico and Texas, where gamma grasses are being displaced by creosote bush (Valentine and Gerard

1968); however, these areas are often so disturbed due to grazing that the native grasses may be too severely stressed to persist anyway.

According to McAuliffe (1984), these nurse-plant relationships may lead to long-term cycles which change the make-up of plant communities in deserts. For instance, where *Opuntia* grows up under creosote bushes, it might outcompete creosote for water or light, causing the creosote to die back locally. But when *Opuntia* ages and dies, creosote may recolonize and eventually serve as a nurse plant, creating a cycle which may be regulated by the life spans of these species. Such a process implies real dynamism in the desert, in which creosote bush plays a part, but not to the exclusion of other plant species.

When creosote bush does not occur in monospecific stands, the plants are often so regularly spaced that it appears as though they might have been planted. It is suggested that this regularity may result from creosotes competing with one another for water, that plants secrete toxic resins into the soil around them which prevent establishment of plants close by, and hence, preserve the local water supply. However, experiments have shown that the soils and plant litter under creosote bushes don't prevent creosote seeds from germinating, and creosote seedlings are on occasion found under adult plants (Barbour 1969, Knipe and Herbel 1966). While competition for water may occur, resulting in the regular patterns observed, "allelochemistry," or toxin production, does not appear to be involved.

Creosote bush has been miscast as a highly aggressive species which regulates the distributions of other plant species and its own by producing chemical toxins or competitive interactions. Rather, it is a species which survives in environments intolerable to most other plant species. As a result, creosote bush provides a refuge and a resource, not only for other plants like the delicate cactus seedlings, but also for many animals. In doing this it helps to define and structure the biological communities of the southwestern deserts.

Creosote bushes often act as "nurse plants" for other species. Cactus seeds rarely germinate in sunny open patches but rather in the shade of plant canopies.

A monospecific stand of creosote bush on a caliche deposit in the Verde Valley.

Over 15 species of native plants have been found growing next to or under the canopies of creosote bushes.

CREOSOTE BUSH AND DESERT ANIMALS

A common sight around creosote bushes is the burrows of numerous lizard and rodent species. Lizards such as whiptails (*Cnemidophorus* spp.), side-blotched lizards (*Uta stansburiana*) and the desert iguana (*Dipsosaurus dorsalis*) commonly use burrows beneath creosote bushes (Mabry et al. 1977). The arboreal tree lizard (*Urosaurus graciosus*) often perches on creosote branches to capture insect prey. This lizard's skin is mottled brown and black, rendering it cryptic on the stems (Mabry et al. 1977). The chuckwalla (*Sauromalus obesus*) feeds occasionally on creosote flowers and fruits, while the desert iguana feeds almost exclusively on creosote flowers when they are available (Norris 1953).

Ten to twelve different species of small mammals are commonly found living in creosote flats in the Southwest (Mabry et al. 1977). These include the jackrabbit (*Lepus californicus*), the desert cottontail (*Sylvilagus audubonii*) kangaroo rats (*Dipodomys* spp.), the grasshopper mouse (*Onychomys* spp.), and the antelope ground squirrels (*Spermophilus* spp.). Creosote bush provides these organisms with improved nesting sites — increased shade, humidity and perhaps protection from predators. Some species, such as kangaroo rats, also feed heartily on creosote seeds (Boyd and Brum 1983) and rabbits feed on branches and small seedlings, particularly following drier winters (Valentine and Gerard 1986; Waring, personal observation).

The flowers of *Larrea tridentata* also attract a large number of insects. These are attracted to the flowers' pollen and nectar. Although individual flowers do not produce unusually large amounts of pollen or nectar (1.88 mg and 0.65mg/flower, respectively, Mabry et al. 1977), individual creosote bushes produce thousands of flowers annually and offer a major food source for animals, because pollen is an excellent source of amino acids (the building blocks of proteins) and nectar provides sugar or energy. Mabry et al. (1977) found over 28 species of bees alone associated with creosote flowers in the Southwest, along with a variety of other insects such as wasps, flies and beetles, in addition to birds. Several species, especially the megachilid bee, *Heteranthidium larreae,* are responsible for most pollination. Male *H. larreae,* actually patrol creosote bushes and the females use leaf resins in the construction of their nests (MacSwain 1946). Each spring as creosote blooms, it attracts insects, small mammals and lizards, providing a food source for many.

A variety of insects also feed on the leaves and stems of creosote bush. Over 40 species of herbivorous insects are partially to wholly dependent on this plant as a food source. Predominant feeders include several species of cryptically colored grasshoppers, butterfly larvae (Geometridae) and a leaf beetle (Chrysomelidae). These

Some animals, such as kangaroo rats, feed heartily on creosote seeds.

chew on leaves. Three species of leafhoppers and several stinkbugs suck sap from the phloem of stems and leaves, and 17 species of midges (mostly *Asphondylia* spp.) form galls on creosote's leaves, stems and flowers. The latter divert the plant's energy into gall formation and then feed on the inside of the gall walls. The gallformers are most abundant on plants which are water stressed (Waring 1986), with densities of galls on stressed plants, such as those in the Grand Canyon, reaching hundreds per branch (Waring, unpublished data). These gallformers have been collected from all parts of creosote's range in the Southwest and may be its commonest natural enemies.

While a great variety of herbivores rely on creosote bush for food, few of them appear to seriously harm the plant. The major exception seems to be the attinine leaf-cutting ants which, in some parts of the Southwest, totally strip creosote bushes of their leaves and flowers, occasionally killing the plants. Overall, however, creosote bush is thriving in the Southwest and herbivore densities remain relatively low. This is somewhat surprising given the abundance of the plant in this region. Several major features of the plant's natural history — its occurrence in the desert and its biochemistry — appear responsible for the relatively low impact of its herbivores.

Desert living makes ample demands on herbivores as well as on the plants they feed on. In the Sonoran Desert, for instance, rainfall occurs in discreet periods during the winter and summer and only during these times do plants grow. Herbivores must be able to quickly take advantage of these growing events and feed on the nutritious tissue plants produce at this time. The gallforming midges on creosote leaves are found only during the spring and later summer monsoon seasons. They must develop quickly during this period of plant growth because if the monsoons end early creosote will begin to drop some of its leaves and galls occurring on dropped leaves will dry out and the gallformers will die. While the periods of precipitation are roughly predictable in the desert, their magnitude and duration are not. Such variability in the midst of harsh conditions makes the desert an even more difficult habitat in which to survive.

Creosote's biochemical products are a story in themselves, and as a result the chemistry of this plant is better studied than most (Mabry et al. 1977). Creosote bush produces powerful compounds which are secreted in resins which prevent most animals from eating it. The leaves secrete these resins whose strong aroma is so common in the spring and following summer rains. They are comprised to a large extent of compounds called phenols, which are digestibility inhibitors. When an animal eats a creosote leaf containing these resins, the phenols bind with the animal's stomach enzymes and prevent them from breaking down proteins contained in the leaves. In experiments, insects which were fed creosote leaves with resins starved to death because of this process, while insects fed leaves with the resins removed survived (Mabry et al. 1977). The insects and vertebrates which do feed on creosote bush do so with limited success or they feed on low resin tissue, such as flowers or older leaves, or else they have evolved adaptations to avoid the effects of the phenols. Interestingly, creosote leaves without resins do represent an ample resource for animals. They contain minerals, carbohydrates and, for desert evergreen plants, very high levels of nitrogen in the form of amino acids and "highly digestible proteins" (Mabry et al. 1977, see also Freeman 1982). However, the resins render them inaccessible to most herbivores.

Ironically, therefore, while creosote bush offers food and refuge to many animals in the Southwest, it protects itself from many others with a powerful defensive biochemistry. This latter feature has probably contributed substantially to the success of creosote bush in our deserts.

CREOSOTE BUSH AND MAN

Creosote bush is of value to man for many practical and aesthetic reasons and apparently this view has been held

Insects form unusual galls on creosote stems, leaves and flowers.

Large drops of lac secreted by the creosote lac insect. Photo courtesy of the Museum of Northern Arizona.

During the rainy season creosote produces many flowers and the characteristic aroma of the desert.

The burrows of numerous lizard and rodent species are a common sight around creosote bushes.

for at least several centuries (Nabhan 1986). The leaves, in particular, have been used by Native Americans in both North and South America and are still used today for many medicinal and other purposes. According to Ms. Phyllis H. Boone, director of the Arizona Ethnobotanical Research Association, most Native American Indian tribes in Arizona, including the Navajo, Hopi, Pima and Papago, use creosote leaves in tea form (often called chaparral tea) in treating maladies. It has been used as an antiseptic for wounds, for liver detoxification, and for colds, arthritis, labor pains and diabetes, to name a few. Nabhan (1986) recounts a story of a woman who, after years of enduring a serious cough, drank chaparral tea and stopped coughing. Perhaps most interestingly, it is used by Hopi medicine men to shrink various cancerous cysts. This latter is also being studied by scientists. One particular phenol produced in creosote resins, nordihydroguaiarectic acid (NDGA), has been shown to reduce tumor growth in laboratory mice (Oliveto 1972, and see Mabry et al. 1977 and Nabhan 1986). NDGA also functions as a powerful antioxidant in preserving food — for instance it can keep vitamin A from breaking down in powdered milk — and in stabilizing rubber. It was used for these purposes in World War II (Nabhan 1986) and today is produced synthetically. The resins and lac have been used to waterproof and repair baskets and fix arrowheads on shafts (Nabhan, Arizona Highways, 1985).

According to Nabhan (1986), creosote bush figures prominently in Papago and Pima Indian lore. Their beautiful stories tell that the noble creosote bush was the first plant to be created on earth; from the plant then came the lac insect which produced lac from which mountains were formed, and the edges of the mountains gave rise to the sky. The Papago and Pima used creosote in many ways in daily life and at death some were buried with sprigs and lac-sealed jars of food (Nabhan 1986).

During World War II, German occupation of the Middle East threatened America's supply of lac, a plant product used for paint, varnish

and record production, and a stateside search for a source of lac was begun. Dr. Harold S. Colton, director of the Museum of Northern Arizona in Flagstaff, undertook a study of the lac-producing scale insect (*Tachardiella larrea*), on creosote bush to learn its life history and determine the economic feasibility of collecting it and using it commercially (Colton 1943). The lac scale sucks phloem juices from the stems of creosote bush and secretes a gummy substance comprised of lac and resins which eventually buries the insect inside, perhaps protecting it from natural enemies. Various companies then tested creosote lac for use in varnish, paint and record production and its chemical properties apparently showed promise. However, Colton found that even in areas where the lac scale was common, it took four men eight hours to collect one pound of lac, rendering the scheme uneconomical.

This plant, a true desert lover, deserves a more prominent place in urban Arizona. It carries with it an exciting history and is highly representative of the Southwest. During the rainy seasons it produces many flowers and the characteristic aroma of the desert, and it attracts many interesting and harmless desert creatures. In the summer heat, it offers a little shade and requires a minimal amount of water. By planting this as an ornamental, people can bring a bit of the desert into their yards and lives. According to Don Feddock (a commercial horticulturist in Ajo, Arizona), creosote bush is a homeowner's dream because it is easy to establish and requires so little care.

Creosote bush helps to define and make up the deserts of the North American Southwest. As a hardy plant which thrives in the desert heat and aridity, it provides habitats and food for many plants and animals. Stop sometime and take a closer look — those creosote flats are teeming with life.

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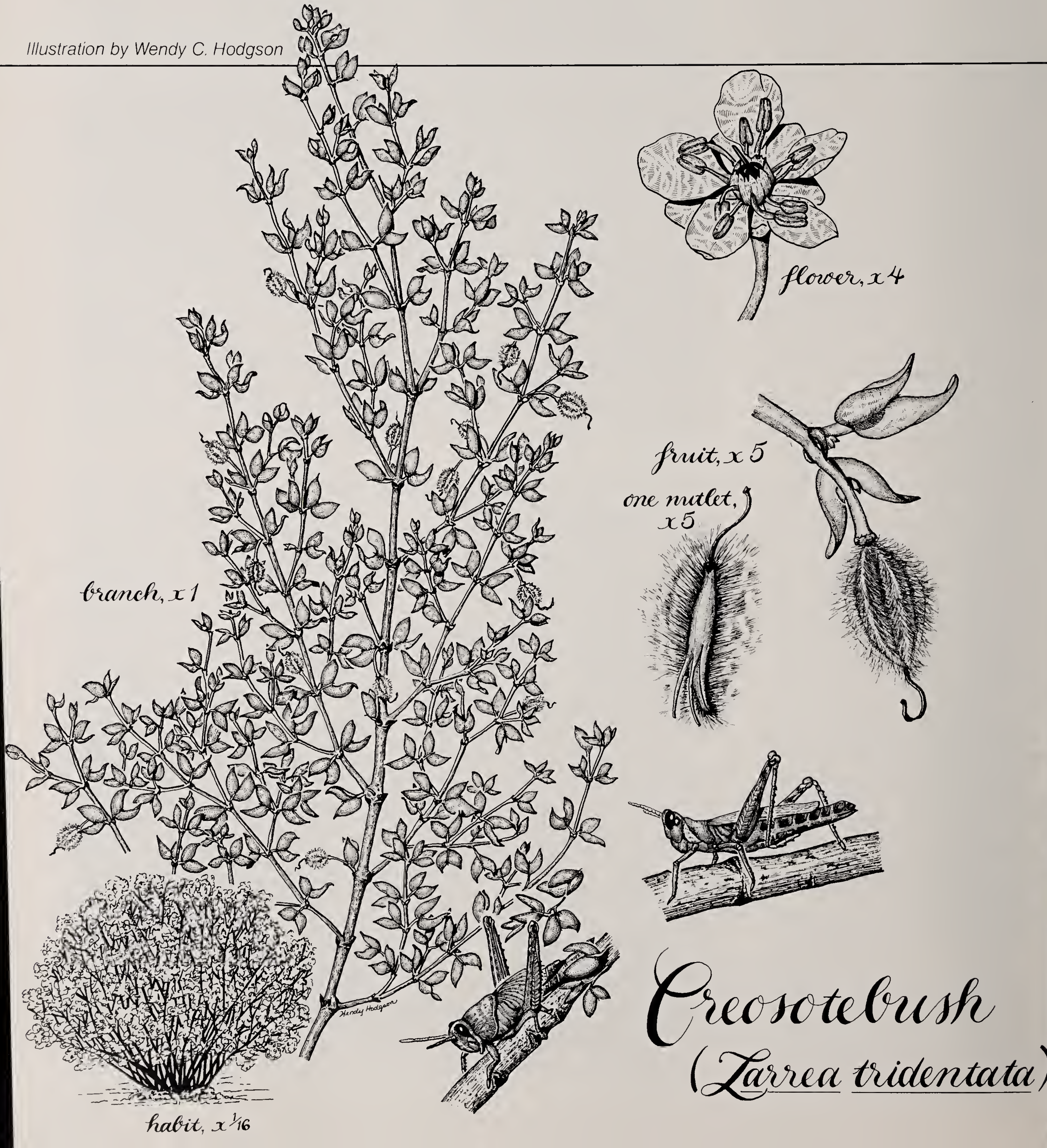

Creosotebush
(Larrea tridentata)